

Effects of competition and mowing on growth and reproduction of the invasive plant *Erigeron annuus* at two contrasting altitudes

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Abstract Invasive plants are often abundant at frequently disturbed sites such as roadsides, because they benefit from reduced competition or increased nutrient availability. In Switzerland, roadsides are subjected to regular mowing, and to persist in these sites, plants must be able to compensate for the biomass removal. However, the ability to tolerate competition and mowing might decline under less favourable growth conditions, such as those at higher altitudes. I investigated how competition and mowing affect growth and reproduction of *Erigeron annuus* (L.) Pers., an invasive plant common on Swiss roadsides, and how these effects change with altitude. The experiment was replicated in common gardens at altitudes of 400 m and 1,000 m asl, representing growth conditions in the main distribution area of *E. annuus* and at its altitudinal limit, respectively. Vegetative growth was negatively affected by competition at both sites, but especially at 1,000 m. The number of capitula was not affected by competition at 400 m, but was reduced at 1,000 m. Plants regrew vigorously after mowing in both gardens. The effects of mowing on reproductive output were positive at 400 m, but negative at 1,000 m. These results imply that *E. annuus* is able to tolerate competition and mowing at low altitudes, but both of these factors hinder its reproduction at higher altitudes.

Zusammenfassung Invasive Neophyten kommen an gestörten Standorten besonders häufig vor, da sie dort weniger Konkurrenz oder eine höhere Nährstoffverfügbarkeit

vorfinden. In der Schweiz sind regelmässig gemähte Strassenränder wichtige Lebensräume und Ausbreitungskorridore für invasive Pflanzen. Offenbar gelingt es den Pflanzen, die Mahdverluste zu kompensieren und sich dennoch zu vermehren. Die Fähigkeit von Pflanzen, Konkurrenz oder Störungen zu ertragen, nimmt in der Regel unter ungünstigen Wachstumsbedingungen ab. Deshalb könnte man erwarten, dass invasive Pflanzen mit zunehmender Meereshöhe aufgrund des kälteren Klimas durch Konkurrenz und Mahd stärker betroffen werden. Hier wurde untersucht, ob Konkurrenz und Mahd das Wachstum und die Fortpflanzung des einjährigen Berufkrauts, *Erigeron annuus* (L.) Pers., je nach Meereshöhe unterschiedlich beeinflussen. Dazu wurde ein Experiment in zwei Gärten auf 400 und 1,000 m ü.M. angelegt, wobei der obere Garten der heutigen Verbreitungsgrenze von *E. annuus* entspricht. Konkurrenz reduzierte das vegetative Wachstum an beiden Orten, jedoch stärker auf 1,000 m. Die Anzahl Blütenköpfe wurde nur auf 1,000 m durch Konkurrenz reduziert. Nach einer Mahd trieben die Pflanzen in beiden Gärten schnell wieder aus. Die Mahd erhöhte die Anzahl Blütenköpfe auf 400 m und senkte sie auf 1,000 m. Diese Ergebnisse bedeuten, dass *E. annuus* in tiefen Lagen Mahd und Konkurrenz ertragen kann, während in höheren Lagen beide Faktoren seiner Ausbreitung entgegenwirken.

Keywords Altitudinal limit · Common garden · Disturbance · Introduced plants · Roadsides · Swiss Alps

Introduction

Many introduced plant species become successful invaders not because they are more competitive than native species, but because they benefit more from nutrient-rich or disturbed conditions associated with human activities (Daehler

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2003). For example, establishment of *Centaurea diffusa*, one of the most problematic introduced plant species in western North America, was shown to be enhanced by high resource availability, and both the densities and size of *C. diffusa* increased when competition was also reduced by partially removing resident grass vegetation (Seastedt and Suding 2007). Similarly, Petryna et al. (2002) observed that the establishment and persistence of six plant species, including *Cirsium vulgare* and *Oenothera erythrosepala* that were introduced from Europe and have become abundant in the mountain grasslands in central Argentina, strongly depended on soil disturbances and aboveground biomass removal by cutting and burning.

Introduced plants may recover better than native ones from biomass removal (Kimball and Schiffman 2003), and mowing or grazing can therefore increase their canopy cover (Brandon et al. 2004). However, a plant's ability for compensatory regrowth generally declines as competition increases and/or nutrient availability decreases (Maschinski and Whitham 1989). In addition, the degree of compensation is also sensitive to the timing of the biomass removal, as clipped plants postpone flowering, and therefore, require a longer vegetation period to reproduce (Lennartsson et al. 1998). Consequently, plants will compensate for biomass removal less well in regions with short growing seasons such as high altitudes and latitudes (Lennartsson et al. 1998). Thus, mowing might serve as an effective management tool to restrict the growth and spread of invasive plants in mountain regions, although it might be ineffective to suppress the species in the lowland regions.

In this study I investigate how competition and mowing affect the growth and reproductive output of the invasive plant *Erigeron annuus* (L.) Pers. (Asteraceae), a winter annual native to North America, but introduced and now widespread in Europe. In Switzerland, *E. annuus* mostly occurs in the lowlands and is rarely found in the Alps above 1,000 m (Becker et al. 2005). It is especially abundant along railways and roads, suggesting that frequent disturbances that reduce competition from resident vegetation might be necessary for its successful establishment. Such sites are also subject to regular mowing, and to persist in these environments *E. annuus* must be able to compensate well for biomass removal. Frey et al. (2003) reported that *E. annuus* regrew well after mowing. They also observed a strong plastic response in leaf shape to the extent where mown plants may sometimes have been misidentified as belonging to another taxon. This plasticity and tolerance to mowing might also have contributed to the species's invasiveness, however, it is unknown whether *E. annuus* is able to maintain its fitness and respond plastically to the mowing under less favourable growth conditions at higher altitudes.

To investigate how *E. annuus* responds to competition and mowing, and whether these responses change with altitude, I conducted a common garden experiment at 400 m and at 1,000 m asl. The lower altitude represented conditions in the main area of *E. annuus* distribution, whereas the higher altitude was close to the current altitudinal limit in Switzerland. I focused on the following questions: (1) How does *E. annuus* respond to competition and mowing? (2) Is its fitness less affected at 400 m than at 1,000 m? (3) Does phenotypic plasticity in response to mowing differ between 400 and 1,000 m?

Materials and methods

Plant material

Erigeron annuus is a winter annual, i.e. seeds usually germinate in late summer and rosettes are formed in autumn. Overwintering rosettes then bolt and flower the following year. The species is triploid ($2n = 27$) and predominantly apomictic, producing a large number (<50,000) of tiny (25 µg), wind-dispersed seeds (Stratton 1989).

Seeds were collected from 35 *E. annuus* plants growing along major roads in the Swiss Alps in August 2004. Plants were at least 2 m apart and originated from 21 different sites ranging from 325 to 965 m. These sites were at least 2 km apart. In the following year, seeds were sown in a common garden at 400 m in order to produce a new generation of seeds free of any maternal effects from their original sites; these seeds were collected in August 2005. Although most populations of *E. annuus* exhibit a high degree of genetic variation, suggesting that sexual reproduction does occasionally occur (Edwards et al. 2006), the seeds from one mother plant are usually genetically identical; therefore, I refer to them as 'clones' hereafter.

Plant cultivation

In December 2005 seeds were germinated on wet filter paper in Petri dishes in a climate chamber (day/night temperatures of 25/16°C). After 10 days seedlings were transplanted into seedling trays filled with standard potting soil (Universalerde Capito, Landi Schweiz). To simulate winter conditions, seedling trays were kept for the next 13 weeks in growth cabinets where day/night temperatures were progressively reduced from 20/12 to 12/4°C. For the next 5 weeks the seedling trays were moved outdoors to the institute terrace, and they were transported to the common gardens at 400 m on 3 May 2006 and at 1,000 m on 5 May 2006. During the experiment the monthly mean

Table 1 Monthly mean temperatures (°C) in the common gardens at 400 m and at 1,000 m asl (M. Zeeman unpubl. data)

	May	June	July	August	September	October
400 m	13.3	17.5	21.7	15.0	16.7	12.4
1,000 m	10.4	14.9	19.4	11.8	14.9	11.1

temperatures were on average 2.4°C higher at 400 m than at 1,000 m (Table 1).

Treatments

Common gardens were set up at the ETH research stations in Chamau (400 m) and Frübüel (1,000 m) in canton Zug, Switzerland. At both sites a fenced area of about 65 m² was ploughed and divided into six plots (3.5 × 1.5 m), which were weeded regularly and treated with molluscicide pellets to protect against slugs. *E. annuus* seedlings were transplanted into two litre plastic pots filled with standard potting soil mixed with perlite (4:1) and slow release NPK fertilizer (Osmocote Exact Standard 8–9 months, Scotts; 0.5 kg per 100 l of soil and perlite mixture). The plants were watered regularly with tap water taken from the same source to ensure identical chemical composition. To reduce the risk of them drying out, the pots were set into the soil to 3/4 of their height. In each plot 35 pots (one per clone) were arranged randomly in four rows.

Three treatments (control, competition and mowing) were applied to two plots per garden. In the plots with the competition treatment, about 0.4 g of grass seeds (Schweizer Uni-Lawn, Eric Schweizer Samen) were sown into the pots at the time of seedling transplant (May 2006). The grass mixture contained 28% of *Lolium perenne*, 45% of *Festuca rubra*, and 27% of *Poa pratensis*. The density and species composition were typical for an ordinary garden lawn. The short stature of the grasses implies that their competitive effect on *E. annuus* was largely limited to below-ground resources. In the plots with mowing treatment, plants were clipped 5 cm above ground (about 90% of shoot mass was removed), when most of them started to flower, i.e. on 22–26 June at 400 m and on 6–12 July at 1,000 m. This timing coincides with the main mowing season for extensively managed grasslands and roadsides in Switzerland.

Plant measurements

Plants were observed weekly to record the dates of important phenological changes—bolting (stem height ≥ 3 cm), formation of flower buds, flowering, and seed set. Vegetative growth was assessed by measuring the number of stems and the number of leaves per stem after most of

the plants started to flower. Additionally, the final height of all plants was measured after seed set. Reproductive output was assessed by collecting all inflorescences (stems with capitula without leaves) of control plants and plants grown with competitors on 15–19 August at 400 m and on 4–10 September at 1,000 m. Inflorescences of mown plants were harvested on 6–8 October at 400 m and on 13–17 October at 1,000 m. At each site the number of capitula was counted on 20 inflorescences in the control and mowing treatments. These were then dried at 70°C and weighed. Based on the linear relationships between inflorescence dry mass and number of capitula, the total number of capitula was estimated for the remaining plants. To assess plasticity in leaf shape, two leaves per clone were sampled from the upper part of the stems of mown plants in one plot per site, both before mowing and after plants had regrown. Photographs of the leaves were used to measure length (*L*) and width (*W*), and the ratio *L/W* was obtained as shape parameter.

Data analyses

To analyse for treatment effects on vegetative growth and reproductive output, analysis of variance was used, where treatment and growth site (i.e. common garden) were treated as fixed factors, and plot (nested within treatment and site) and clone were treated as random factors. Due to non-normal distribution, data for the number of stems, the number of capitula per stem and the total number of capitula were square root transformed. The means of the treatments were compared to that of the control using Dunnett's method. Two-way analysis of variance was used to test for the effects of mowing, growth site and their interaction on leaf morphology.

For the plant phenology data, I performed survival analyses. The numbers of days to bolting, formation of flower buds, flowering and seed set were analysed by fitting survival curves with a Weibull distribution separately for each phenological transition. If a phenological transition was not reached, the observation was censored. The expected number of days needed for 50% of the plants to reach each phenological transition at either growth site was estimated separately for each treatment using survival models. All statistical analyses were performed in JMP 7.0.1 (SAS Institute Inc. 2007).

Results

All plants survived and grew well, but their performance was strongly affected by both the experimental treatments and the growth sites (Table 2). In all treatments, the number of stems, the total number of leaves and the total

Table 2 ANOVA results (F , P) for the fixed effects of treatment (Control, Competition, Mowing), growth site (400 m, 1,000 m asl) and their interaction on vegetative growth and reproductive output of *E. annuus*

	Treatment (T)	Site (S)	$T \times S$
Number of stems	132.37***	51.46***	3.56
Leaves per stem	586.82***	67.21***	31.50**
Total number of leaves	17.72**	24.38**	4.91 ^{0.051}
Final height	27.79***	10.42	5.94*
Capitula per stem	16.79**	2.99*	0.52
Total number of capitula	0.13	50.93***	3.17

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$

number of capitula were lower at 1,000 m than at 400 m (Table 3). Control plants and plants grown with competitors tended to grow taller and have more leaves per stem at 1,000 m than at 400 m (i.e. significant treatment by site interactions in Table 2), but this was not the case for the mown plants.

The effect of competition on vegetative growth and reproduction was stronger at 1,000 m than at 400 m (Table 3). Compared to control plants, competition reduced the number of stems by 19% at 400 m, but by 38% at 1,000 m. The fewer stems did not lead to a lower reproductive output of plants with competitors at 400 m, because more capitula were produced per stem. However, at 1,000 m competition reduced the reproductive output by 13% compared to control plants.

Mowing led to a vigorous regrowth in both common gardens (Table 3). Mown plants produced 127 and 86% more stems than control plants at 400 m and at 1,000 m, respectively. The effects of mowing on reproductive output were positive at 400 m, but negative at 1,000 m due to a strong decrease in the number of capitula per stem. Mown plants produced 28% more capitula than control plants at 400 m, but 28% fewer at 1,000 m.

Leaf shape differed significantly between the two common gardens. Before mowing, leaves were narrower at 1,000 m than at 400 m (length (L)/width (W) = 3.57 ± 0.08

(SE) vs. 3.09 ± 0.08 ; $F_{1,136} = 4.1$, $P = 0.044$). Mowing had a significant effect on *E. annuus* leaf shape ($F_{1,136} = 21.1$, $P < 0.0001$), but this effect differed between altitudes ($F_{1,136} = 11.9$, $P = 0.0008$). At 400 m the leaves produced after mowing ($L/W = 3.79 \pm 0.10$) were narrower than before (Fig. 1), but this was not the case at 1,000 m ($L/W = 3.67 \pm 0.09$).

All plants flowered and reproduced, except for two mown plants at 1,000 m, which had flowered but not produced seeds by the end of the experiment (October 2006). Phenology was not influenced by competition, but seed set was postponed by mowing (Fig. 2). In all treatments, development was slower at 1,000 m than at 400 m (Fig. 2). Based on the estimated number of days for 50% of the plants to reach a phenological transition, the onset of seed production at 1,000 m was delayed by 19, 22 and 50 days in the control, competition and mowing treatment, respectively (Fig. 2).

Discussion

Effect of competition on growth and reproduction

Competition with grasses reduced the vegetative growth and reproductive output of *E. annuus* more at 1,000 m than at 400 m. These results indicate that *E. annuus* can tolerate competition better at low altitudes than at higher altitudes, and therefore, its distribution at higher altitudes will probably be restricted to disturbed sites.

Other invasive plants have also been shown to be negatively affected by competition with native species and constrained to disturbed areas (Sala et al. 2007). However, some species may enhance their invasiveness by an adjustment of their phenology. For instance, the survival of two introduced plants, *Senecio inaequidens* and *S. pterophorus* that recently invaded protected areas in Catalonia (Spain), was dramatically reduced by resident vegetation when the establishment occurred in the spring, but not when the plants established in autumn, probably due to

Table 3 Means (SE) of vegetative growth and reproductive output of *E. annuus* in different treatments at either growth site

	400 m			1,000 m		
	Control	Competition	Mowing	Control	Competition	Mowing
Number of stems	9.6 ± 0.3	$7.8 \pm 0.3^*$	$21.8 \pm 0.7^*$	7.7 ± 0.3	$4.8 \pm 0.3^*$	$14.3 \pm 0.5^*$
Leaves per stem	25.2 ± 0.3	26.1 ± 0.4	$15.2 \pm 0.2^*$	29.6 ± 0.5	29.3 ± 0.5	$15.1 \pm 0.4^*$
Total number of leaves	239.9 ± 8.0	$202.2 \pm 8.3^*$	$327.9 \pm 9.8^*$	226.3 ± 8.1	$137.0 \pm 6.8^*$	210.7 ± 7.9
Final height (cm)	107.9 ± 1.4	$113.2 \pm 1.5^*$	104.5 ± 1.5	117.8 ± 1.3	118.5 ± 1.6	$102.6 \pm 1.1^*$
Capitula per stem	350.8 ± 24.6	$464.5 \pm 34.1^*$	$197.5 \pm 11.1^*$	266.8 ± 13.8	$447.7 \pm 42.4^*$	$106.0 \pm 4.2^*$
Total number of capitula	$3,189 \pm 167$	$3,312 \pm 167$	$4,088 \pm 196^*$	$1,947 \pm 83$	$1,700 \pm 78^*$	$1,404 \pm 50^*$

Asterisks indicate that the comparison with the respective control was significant at a level of $P < 0.05$

Fig. 1 Leaves sampled from the mid stems of the same clones at 400 m (a) before and (b) after mowing, and at 1,000 m (c) before and (d) after mowing

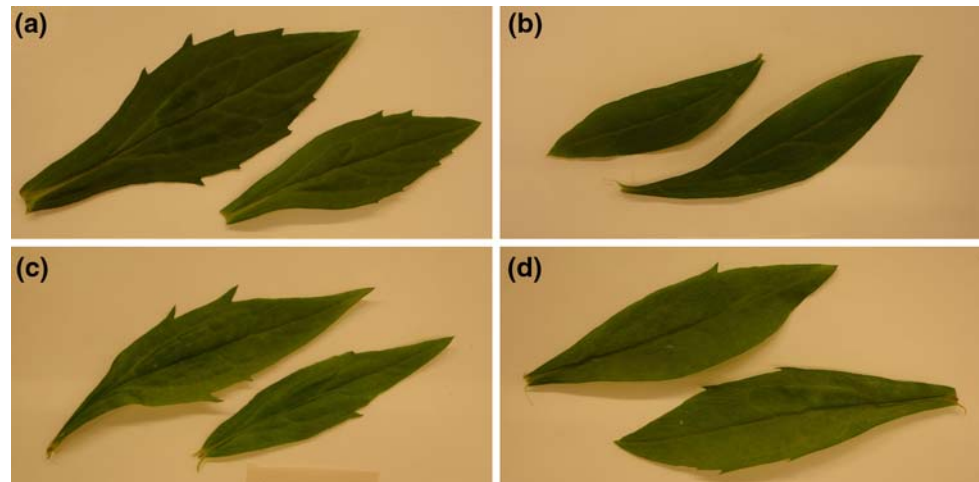
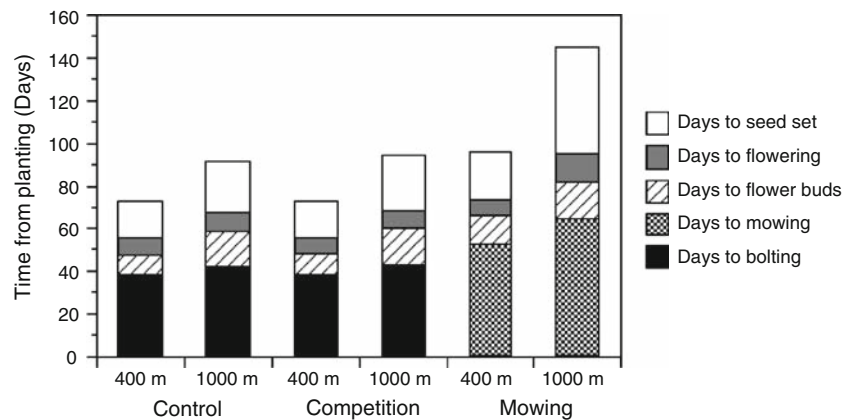


Fig. 2 Time estimates for 50% of the plants to reach different phenological transitions at 400 and 1,000 m, as derived from survival models. Seedlings were planted at 400 m on 3 May and at 1,000 m on 5 May. Plants were mown when most of them started to flower



higher water availability (Cano et al. 2007). *E. annuus* usually produces seeds in autumn and overwinters as vegetative rosettes. Regehr and Bazzaz (1976) found that photosynthesis over winter enables *E. annuus* to accumulate energy reserves and gives the species competitive advantage over plants that germinate in spring. This ability might enhance the establishment of *E. annuus* even in more closed habitats.

A limitation of my study is that the competition treatment took place in nutrient-rich conditions and was only imposed after the seedlings had established. Competitive interactions between plants might be influenced by the initial size of competing individuals, and initially larger plants might be misjudged as competitively superior (Gibson et al. 1999; Connolly et al. 2001). The relative times at which plants establish may also play a role, as would be the case if the first plants to establish had a competitive advantage over those coming later (Ross and Harper 1972; White and Holt 2005). My results do therefore not imply that *E. annuus* would be able to establish and persist in dense vegetation, as it might be outcompeted in its early life stages. However, in habitats with gaps

available for its initial establishment, it is able to reproduce and maintain a population, especially at low altitudes.

Effect of mowing on growth and reproduction

At 400 m mown *E. annuus* plants overcompensated both in terms of vegetative growth and reproductive output. Similar responses have been observed in other monocarpic plants grown without competition in high nutrient environments (Maschinski and Whitham 1989; Huhta et al. 2000), although such responses seem to be species specific (Moreno et al. 1999) and depend very much on plant architecture and position of meristems (Kimball and Schiffman 2003). Induction of overcompensation might also be restricted to a relatively short period of time, where the early limit is determined by the amount of resources available for regrowth, and the late limit depends on phenology and the amount of undifferentiated meristems (Lennartsson et al. 1998). However, in their old-field experiment, Joshi and Matthies (1996) did not observe any significant reduction in the cover of *E. annuus* even after 5 years of annual mowing. Therefore, the spread of

E. annuus would probably not be prevented by mowing in the lowland regions.

In contrast, mowing might hinder *E. annuus* establishment at higher altitudes, as it strongly delayed plant phenology at 1,000 m. Seed set in mown plants was postponed to the end of September, while control plants reproduced at the beginning of August. Therefore, there might not be enough time for seed germination and rosette formation before the onset of winter, which might strongly reduce the number of newly establishing plants. However, in another experiment I observed that the seed germination might be postponed to the following spring and that the annual life cycle changed to biennial (Trtikova et al. unpublished data). Thus, in disturbed sites at higher altitudes mowing might delay, but not prevent the spread of *E. annuus*.

Effect of mowing on leaf shape

I could confirm the observation of Frey et al. (2003) that in the lowlands mown *E. annuus* plants produced narrower leaves than unmown plants. Such a change in leaf morphology directly affects photosynthetic and respiratory capacities of the plants and might facilitate their regrowth (Fahnestock and Detling 2000). At 1,000 m however, the leaf shape of *E. annuus* was not affected by mowing, possibly because it was primarily determined by climatic conditions. In another experiment with *E. annuus*, I observed that rosette leaf traits, including specific leaf area, changed with altitude (Trtikova et al. unpublished data). I found no evidence that this was due to local adaptation, therefore, these responses are rather attributable to phenotypic plasticity that could enable *E. annuus* to better tolerate harsher climatic conditions at higher altitudes. Due to *E. annuus*' large plasticity in leaf shape, not only plants exposed to mowing, but also those originating from higher altitudes may have been mistakenly identified as a distinct taxon (i.e. *E. annuus* var. *septentrionalis*; Frey et al. 2003).

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